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IPSENOL: AN AGGREGATION PHEROMONE FOR *Ips latidens* (LECONTE) (COLEOPTERA: SCOLYTIDAE)

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Abstract—Ipsenol was identified from the frass of male, but not female, *Ips latidens* from British Columbia, feeding in phloem tissue of lodgepole pine, *Pinus contorta* var. *latifolia*. The responses of *I. latidens* to sources of ipsenol and *cis*-verbenol were determined with multiple-funnel traps in stands of lodgepole pine in British Columbia. Ipsenol attracted both male and female *I. latidens*, verifying that it is a pheromone for this species. Male *I. latidens* showed a slight preference for (*S*)-(−)-ipsenol. *cis*-Verbenol was not produced by beetles of either sex and, in contrast to an earlier report, both enantiomers inhibited attraction to ipsenol-baited traps. The predators, *Enoclerus sphegeus* and *Thanasimus undatulus* (Cleridae), were attracted to traps baited with *cis*-verbenol and ipsenol.

Key Words—Pheromone, ipsenol, *cis*-verbenol, chirality, *Ips latidens*, Coleoptera, Scolytidae, predator, kairomone, *Enoclerus sphegeus*, *Thanasimus undatulus*, Cleridae.

INTRODUCTION

In British Columbia, the bark beetle, *Ips latidens* (LeConte) (Coleoptera: Scolytidae), feeds and breeds in the phloem tissue of lodgepole and ponderosa pines, *Pinus contorta* var. *latifolia* Engelmann and *P. ponderosa* Douglas ex Lawson

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and Lawson, respectively (Bright, 1976; Furniss and Carolin, 1980; Wood, 1982). Like many other bark beetles, *I. latidens* has the potential to be a significant pest in stands of lodgepole pine, particularly in association with the mountain pine beetle, *Dendroctonus ponderosae* Hopkins (Scolytidae), or during periods of chronic drought (Furniss and Carolin, 1980; Miller and Borden, 1985).

Ipsenol (2-methyl-6-methylene-7-octen-4-ol) has been implicated as a pheromone for *I. latidens* in California. *Ips latidens* were caught, albeit in low numbers, on traps baited with either ipsenol or a mixture of ipsenol and *cis*-verbenol (*cis*-4,6,6-trimethylbicyclo[3.1.1]hept-3-en-2-ol) (Wood et al., 1967). In Idaho, *I. latidens* were attracted to sources of racemic ipsenol; alone and in combination with bolts of ponderosa pine (Furniss and Livingston, 1979). However, the question of whether ipsenol is a pheromone for *I. latidens* is still unresolved since the production of ipsenol by *I. latidens* has not yet been determined.

Our objective was to determine the identity of pheromone(s) used by *I. latidens* in stands of lodgepole pine in British Columbia. Various scolytid species show behavioral responses to different enantiomers of ipsenol and the related chiral alcohol, ipsdienol (2-methyl-6-methylene-2,7-octadien-4-ol) (Borden, 1982). Therefore, we tested the three following hypotheses: (1) one or both sexes of *I. latidens* would produce one or both enantiomers of ipsenol and/or one or both enantiomers of *cis*-verbenol; (2) *I. latidens* would be attracted to chiral ipsenol; and (3) *cis*-verbenol would act synergistically in increasing attraction of *I. latidens* to chiral ipsenol. Concurrent research by Seybold et al. (1991) tested similar hypotheses for *I. latidens* in California, breeding in ponderosa pine.

METHODS AND MATERIALS

In 1984, adult *I. latidens* were obtained from a 2-year-old colony that originated near the east gate of Manning Park, British Columbia. Using the gelatin-pill-capsule technique (Borden, 1967), 16 adult males and five adult females were restrained, individually, on noninfested bolts of lodgepole pine, collected near Princeton, British Columbia. Beetles were allowed to bore into the bark and feed for 24 hr. The frass of each individual was crushed in 150 μl of pentane. These extracts were analyzed by splitless capillary gas chromatography (Hewlett Packard HP 5890 using a 30-m $\times$ 0.25-mm-ID fused silica column). The identities and integrities of ipsenol and *cis*-verbenol were verified by mass spectrometry using splitless capillary gas chromatography (Hewlett Packard HP 5985B).

Racemic ipsenol (chemical purity, 98%) was obtained from Bedoukian

Research Inc. (Danbury, Connecticut). B.J. Johnston (Department of Chemistry, Simon Fraser University, Burnaby, British Columbia) supplied chiral ipsenols (optical purities, 96% (*S*)-(−) and 94% (*R*)-(+), respectively; chemical purities, 98%). (−)-β-Phellandrene was obtained from the SCM Corporation (Jacksonville, Florida).

Phero Tech Inc. (Vancouver, British Columbia) supplied polyethylene, bubble-cap devices containing the following chemicals: (1) racemic ipsenol (chemical purity, 98%) in solution with 1,3-butanediol; (2) 1,3-butanediol (chemical purity, >98%); (3) ethanol (chemical purity, 99%); and (4) chiral *cis*-verbenols (optical purities, 84% (*S*)-(−) and 94% (*R*)-(+), respectively; chemical purities, 98%).

β-Phellandrene was released from closed, polyethylene, microcentrifuge tubes (1.8 ml) (Evergreen Scientific, Los Angeles, California). The release rate was approximately 8 mg/day at 27–30°C (determined by weight loss). Ipsenol release devices consisted of either 10-cm lengths of C-flex tubing (ID = 1.6 mm; OD = 2.4 mm) (Concept Inc., Clearwater, Florida) filled with a solution of ipsenol in ethanol, or polyethylene, bubble-cap devices filled with a solution of ipsenol in 1,3-butanediol, and heat-pressure sealed. The release rates of ipsenol from these devices were approximately 0.6 and 0.2–0.3 mg/day, respectively, at 24°C (determined by collection of volatiles on Porapak-Q). 1,3-Butanediol was not released from either C-flex or bubble-cap lures. Ethanol release devices consisted of either 10-cm lengths of C-flex tubing or polyethylene bubble-caps, each filled with ethanol and heat-pressure sealed. The release rates of ethanol from these devices were approximately 10 and 6 mg/day, respectively, at 24°C (determined by weight loss). *cis*-Verbenol was released from polyethylene, bubble-cap devices at a rate of 3–6 mg/day at 27–30°C (determined by weight loss).

In all experiments, eight-unit, multiple-funnel traps (Lindgren, 1983) (Phero Tech) were set in mature stands of lodgepole pine near Princeton, British Columbia. Each trap was suspended such that the top funnel of each trap was 1.3–1.5 m above ground. No trap was within 2 m of any tree. Treatments were assigned randomly within replicates. Sexes of *I. latidens* captured in experiment 1 were determined by dissection and examination of genitalia. Sexes of *I. latidens* captured in other experiments were not determined due to insufficient numbers for most of the treatments. Sexes of other beetles caught in traps were not determined.

In experiments 1–3, replicate grids were placed at least 100 m apart, and traps were spaced 10–15 m apart within each replicate. The effect of chiral ipsenol was tested in experiment 1. Eleven replicates of six traps per replicate, were set in grids of 2 × 3, from May 23 to July 2, 1987. The treatments, using C-flex devices, were as follows: (1) blank control; (2) ethanol control; (3) racemic ipsenol (0.6 mg/day); (4) racemic ipsenol (1.2 mg/day); (5) (*S*)-(−)-

ipsenol (0.6 mg/day); and (6) (*R*)-(+)-ipsenol (0.6 mg/day). All ipsenol devices contained ethanol.

Experiment 2 tested the effects of ethanol and the interaction between ipsenol and ethanol. Seven replicates of four traps per replicate were set in grids of 2 × 2, from August 6 to 31, 1989. The treatments, using bubble-cap devices, were as follows: (1) 1,3-butanediol; (2) ethanol and 1,3-butanediol (as two separate devices); (3) racemic ipsenol; and (4) racemic ipsenol and ethanol (as two separate devices). All ipsenol devices contained 1,3-butanediol.

Experiment 3 tested for interaction between (*S*)-(−)-*cis*-verbenol and the combination of ipsenol and β-phellandrene. β-Phellandrene is used as a kairomone by *I. latidens* (Miller and Borden, 1990). Nine replicates of four traps per replicate were set in grids of 2 × 2, from May 21 to June 23, 1988. The treatments, using C-flex devices, were as follows: (1) ethanol control; (2) racemic ipsenol and β-phellandrene (as two separate devices); (3) (*S*)-(−)-*cis*-verbenol; and (4) the combination of racemic ipsenol, β-phellandrene, and (*S*)-(−)-*cis*-verbenol (as three separate devices). All ipsenol devices contained ethanol.

Experiment 4 tested for interaction between (*R*)-(+)-*cis*-verbenol and ipsenol. β-Phellandrene was not used due to lack of availability. Traps were placed 50 m apart in a single, large grid pattern measuring 200 × 400 m. Ten replicate blocks of four linearly consecutive traps per block were set along parallel trap lines, spaced 50 m apart, from June 21 to July 10, 1989. The treatments, using bubble-cap lures, were as follows: (1) 1,3-butanediol; (2) racemic ipsenol; (3) (*R*)-(+)-*cis*-verbenol; and (4) racemic ipsenol and (*R*)-(+)-*cis*-verbenol (as two separate devices). All ipsenol devices contained 1,3-butanediol.

The data were analyzed using the SAS statistical package version 5.0 (SAS Institute Inc., Cary, North Carolina). Trap catches of all species were transformed by $\ln(Y + 1)$ to remove heteroscedasticity. Sex ratio data for *I. latidens* were normalized by an arcsin transformation. Homoscedastic data were subjected to either one-, two-, or three-way analysis of variance (ANOVA). Evidence of synergy in the attraction of beetles, due to the interaction of multiple components, was determined by the interaction term in ANOVA. Two multiple contrasts were performed in experiment 1. Ryan-Einot-Gabriel-Welsch (REGW) multiple-range tests were used in experiments 2–4 when $P < 0.05$.

RESULTS AND DISCUSSION

Ipsenol is a pheromone for *Ips latidens*. It was found in the frass of 10 of 16 male *I. latidens* (estimated range, 10 ng to 1 mg), but not in the frass of any female. The chirality of ipsenol was not determined because we were unable to separate the acetyl lactate diastereomers (Slessor et al., 1985) of synthetic racemic ipsenol by gas chromatography. *cis*-Verbenol was not found in any samples. Similar results were found by Seybold et al. (1991) for Californian *I. latidens*. The major monoterpene in the frass was β-phellandrene. β-Phellandrene is the major monoterpene in the phloem tissue of lodgepole pine (Mirov, 1961; Shrimpton, 1972, 1973) and is a kairomone for *I. latidens* (Miller and Borden, 1990).

In experiments 1 and 2, *I. latidens* were significantly attracted to ipsenol, with a slight preference for (*S*)-(−)-ipsenol (Figures 1A and 2). The results in

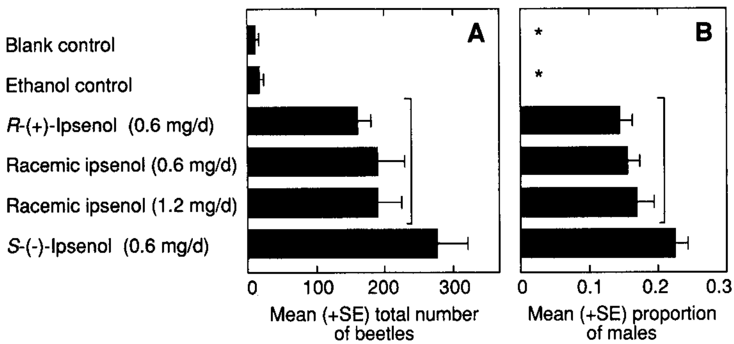

FIG. 1. The effect of chiral ipsenol on the number (A) and sex ratio (B) of *Ips latidens* responding to multiple-funnel traps near Princeton, British Columbia, in experiment 1 from May 23 to July 2, 1987 ($N = 11$). Mean numbers grouped by a line are significantly different from the blank and ethanol controls as well as (*S*)-(−)-ipsenol [multiple contrasts, $F(1,49)$, $P < 0.001$ and $P = 0.025$, respectively, on data transformed by $\ln(Y + 1)$]. Mean proportions of males grouped by a line are significantly different from (*S*)-(−)-ipsenol [multiple contrast, $F(1,30)$, $P = 0.008$, on data transformed by $\arcsin(Y)$]. Some treatments (*) had insufficient numbers for determinations of sex ratios.

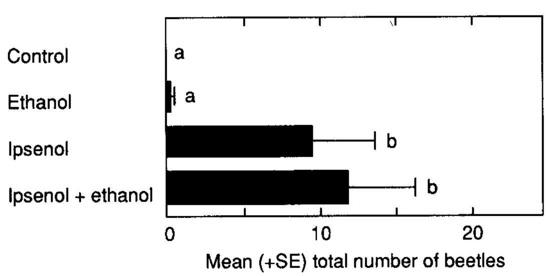

FIG. 2. The effect of ethanol and ipsenol on the attraction of *Ips latidens* to multiple-funnel traps near Princeton, British Columbia, in experiment 2 from August 6 to September 2, 1989 ($N = 7$). Means followed by the same letter are not significantly different at $P = 0.05$ [REGW multiple range test on data transformed by $\ln(Y + 1)$].

experiment 1 can be attributed solely to ipsenol, since ethanol alone was not attractive and there was no significant interaction between ethanol and ipsenol in experiment 2 [ANOVA, $F(1,24)$, $P = 0.441$ and $P = 0.989$, respectively]. The sex ratios of *I. latidens* captured in experiment 1 were affected by chirality [ANOVA, $F(3,30)$, $P = 0.048$]. Proportionally more males responded to (*S*)-(−)-ipsenol than to either racemic or (*R*)-(+)-ipsenol (Figure 1B). Our results agree with the field data of Wood et al. (1967) and Furniss and Livingston (1979) and recent laboratory data of Seybold et al. (1991).

In contrast to results from California (Wood et al., 1967), both enantiomers of *cis*-verbenol inhibited the response of *I. latidens* to sources of ipsenol (Figures 3 and 4). *cis*-Verbenol was not produced by male *I. latidens*. *cis*-Verbenol is produced by sympatric species of bark beetles such as *D. ponderosae* (Pierce et al., 1987; Libbey et al., 1985) and may act as a synomone

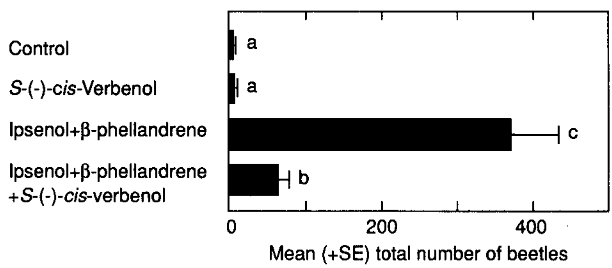

FIG. 3. The effect of (*S*)-(−)-*cis*-verbenol and the combination of ipsenol and β-phellandrene on the attraction of *Ips latidens* to multiple-funnel traps near Princeton, British Columbia, in experiment 3 from June 8 to 23, 1988 ($N = 9$). All treatments contained ethanol. Means followed by the same letter are not significantly different at $P = 0.05$ [REGW multiple range test on data transformed by $\ln(Y + 1)$].

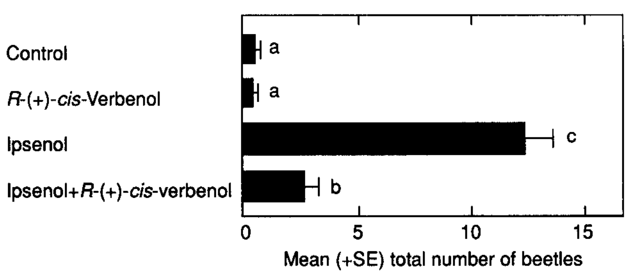

FIG. 4. The effect of (*R*)-(+)-*cis*-verbenol and ipsenol on the attraction of *Ips latidens* to multiple-funnel traps near Princeton, British Columbia, in experiment 4 from June 21 to July 10, 1989 ($N = 10$). Means followed by the same letter are not significantly different at $P = 0.05$ [REGW multiple range test on data transformed by $\ln(Y + 1)$].

(Nordlund and Lewis, 1976), facilitating resource partitioning and minimizing interspecific competition for phloem tissue. The role of synomones in cross-attraction and host partitioning has been demonstrated in bark beetle communities such as the loblolly pine, *P. taeda* L., community of southern pine beetles in the southern United States (Hedden et al., 1976; Vité et al., 1978; Dixon and Payne, 1979; Birch et al., 1980; Svihra et al., 1980; Paine et al., 1981; Watterson et al., 1982).

Sources of ipsenol and/or *cis*-verbenol and/or ethanol also were attractive to other species of bark beetles. In experiment 1, *Ips mexicanus* (Hopkins) preferred traps baited with ipsenol, regardless of chirality or release rate (Table 1). The treatment with the highest release rates of ipsenol and ethanol were preferred by *Hylurgops porosus* (LeConte) and a *Pityophthorus* Eichhoff species. Unlike the *Pityophthorus* species, *H. porosus* was attracted to ipsenol alone. *Hylastes longicollis* Swaine did not exhibit any preferences in experiment 1. However, in experiment 3, ipsenol with β-phellandrene was the preferred treatment for *H. longicollis* as well as for *I. mexicanus* and a *Pityophthorus* species (Table 2). *Hylurgops porosus* showed equal preference for the combinations of ipsenol and β-phellandrene, and ipsenol with β-phellandrene and (S)-($-$)-*cis*-verbenol.

TABLE 1. EFFECTS OF CHIRAL IPSENOL ON ATTRACTION OF *Ips mexicanus, Hylastes longicollis, Hylurgops porosus*, AND A *Pityophthorus* sp. (SCOLYTIDAE) TO MULTIPLE-FUNNEL TRAPS NEAR PRINCETON, BRITISH COLUMBIA, IN EXPERIMENT 1, MAY 23 TO JULY 2, 1987 (N = 11)

Treatment	Mean ($\pm$SE) total number of beetles[a]			
	Ips mexicanus	*Hylastes longicollis*[b]	*Hylurgops porosus*	*Pityophthorus* species
Blank control	0.1 ± 0.1 a	6.3 ± 1.4	12.9 ± 4.2 a	5.7 ± 3.1 a
Ethanol	0.1 ± 0.1 a	8.7 ± 1.8	23.0 ± 5.3 bc	4.0 ± 1.9 a
Ethanol + (R)-(+)-ipsenol (0.6 mg/day)	2.8 ± 1.1 b	7.9 ± 1.2	25.3 ± 4.6 bc	7.4 ± 2.1 ab
Ethanol + racemic ipsenol (0.6 mg/day)	2.5 ± 0.7 b	6.3 ± 1.3	22.8 ± 5.1 bc	7.8 ± 1.8 ab
Ethanol + racemic ipsenol (1.2 mg/day)	2.4 ± 0.9 b	9.0 ± 1.7	31.7 ± 4.9 c	13.3 ± 3.7 b
Ethanol + (S)-($-$)-ipsenol (0.6 mg/day)	2.5 ± 0.9 b	5.8 ± 1.4	19.2 ± 4.0 b	3.3 ± 0.8 a

[a] Means within a column followed by different letters are significantly different at P = 0.05 [REGW multiple range test on data transformed by $\ln(Y + 1)$].
[b] No significant differences among means [ANOVA, $F(5, 49)$, P = 0.232].

TABLE 2. EFFECTS OF (*S*)-(−)-*cis*-VERBENOL AND COMBINATION OF RACEMIC IPSENOL AND β-PHELLANDRENE ON ATTRACTION OF *Ips mexicanus*, *I. perturbatus*, *Hylastes longicolis*, *Hylurgops porosus*, A *Pityphthorus* SPECIES (SCOLYTIDAE), AND *Enoclerus sphegeus* (CLERIDAE), TO MULTIPLE-FUNNEL TRAPS NEAR PRINCETON, BRITISH COLUMBIA, IN EXPERIMENT 3, JUNE 8–23, 1988 ($N = 7$)

	Mean (± SE) total number of beetles[a]					
Teatment	*Ips mexicanus*	*Ips perturbatus*	*Hylastes longicollis*	*Hylurgops porosus*	*Pityophthorus* species	*Enoclerus sphegeus*
Ethanol	0.2 ± 0.2 a	0.8 ± 0.5 a	3.8 ± 0.6 a	9.0 ± 3.5 a	0.8 ± 0.3 a	0.7 ± 0.7 a
Ethanol + (*S*)-(−)-*cis*-verbenol	2.0 ± 0.6 b	1.4 ± 0.9 a	5.1 ± 1.8 a	8.6 ± 1.7 a	1.3 ± 0.4 a	5.3 ± 1.6 bc
Ethanol + ipsenol + β-phellandrene	18.9 ± 3.5 c	1.4 ± 0.8 a	11.4 ± 2.5 b	21.3 ± 3.0 b	11.1 ± 3.0 b	1.8 ± 0.7 ab
Ethanol + ipsenol + β-phellandrene + (*S*)-(−)-*cis*-verbenol	3.3 ± 0.5 b	1.9 ± 3.7 b	3.9 ± 1.2 a	14.6 ± 3.9 ab	2.1 ± 1.2 a	15.0 ± 5.1 c

[a]Means within a column followed by different letter are significantly different at $P = 0.05$ [REGW multiple-range tests on data transformed by $\ln(Y + 1)$].

Explanations for significant treatment differences in these species must be viewed as speculative. Responses by bark beetles suggest that ipsenol and/or *cis*-verbenol are used as either pheromones or synomones (Tables 1 and 2). However, there are no data on the phenology of pheromone production by any of these species. The low numbers caught in traps, relative to *I. latidens*, may be a consequence of four factors: (1) low population numbers; (2) missing pheromones; (3) other semiochemical functions; or (4) random chance.

The experimental areas were selected for abundance of *I. latidens*. We have no data on the abundance of the other species. However, *I. pini* (Say) and *Pityogenes knechteli* Swaine were very abundant in both years but neither was trapped. Ipsenol inhibits the response of *I. pini* to suitable hosts and to its own pheromone, ipsdienol (Birch and Light, 1977; Birch et al., 1977; Furniss and Livingston, 1979). It seems reasonable to hypothesize that ipsenol and/or *cis*-verbenol are also inhibitory to *P. knechteli*, or have no effect.

The preferred treatment for the clerid (Coleoptera), *Enoclerus sphegeus* F., in experiment 3 was the combination of ipsenol with ethanol, β-phellandrene and (*S*)-(−)-*cis*-verbenol (Table 2). The interaction between treatments had an additive, not synergistic, effect on the attraction of *E. sphegeus* [ANOVA, $F(1,24)$, $P = 0.822$]. In experiment 4, both *E. sphegeus* and *Thanasimus undatulus* Say (Cleridae) preferred the combination of ipsenol and (*R*)-(+)-*cis*-verbenol over all other treatments (Table 3). The interaction between ipsenol and (*R*)-(+)-*cis*-verbenol had a synergistic effect on the attraction of *E. sphegeus* [ANOVA, $F(1,36)$, $P = 0.001$] but an additive effect on the attraction of *T. undatulus* [ANOVA, $F(1,36)$, $P = 0.560$].

TABLE 3. EFFECTS OF (*R*)-(+)-*cis*-VERBENOL AND RACEMIC IPSENOL ON ATTRACTION OF *Enoclerus sphegeus* AND *Thanasimus undatulus* (CLERIDAE) TO MULTIPLE-FUNNEL TRAPS NEAR PRINCETON, BRITISH COLUMBIA, IN EXPERIMENT 4, JUNE 21 TO JULY 10, 1989 ($N = 10$)

	Mean (± SE) total number of beetles[a]	
Treatment	*Enoclerus sphegeus*	*Thanasimus undatulus*
Blank control	0.1 ± 0.1 a	0.1 ± 0.1 a
(*R*)-(+)-*cis*-Verbenol	0.2 ± 0.1 a	2.5 ± 1.0 b
Ipsenol	1.2 ± 0.3 b	2.3 ± 0.5 b
Ipsenol + (*R*)-(+)-*cis*-verbenol	5.9 ± 0.9 c	6.0 ± 1.1 c

[a] Means within a column followed by different letters are significantly different at $P = 0.05$ [REGW multiple range tests on data transformed by $\ln(Y + 1)$].

Responses by the clerids, *E. sphegeus* and *T. undatulus*, to sources of *cis*-verbenol and the combination of ipsenol and *cis*-verbenol (Tables 2 and 3) are consistent with other studies demonstrating the use of bark beetle pheromones as kairomones by predators (Borden, 1982; Dahlsten, 1982). The lack of specificity in prey of *E. sphegeus* is exemplified by its capacity to respond to pheromones of other species such as *exo*-brevicomin produced by *Dendroctonus* and *Dryocoetes* species (Borden et al., 1987).

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